

## SPERMATOPHORES AND THE EVOLUTION OF FEMALE GENITALIA IN WHIP SPIDERS (CHELICERATA, AMBLYPYGI)

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**ABSTRACT.** Whip spiders use stalked spermatophores for sperm transfer. These are complex structures, and their morphology varies among genera and families. Usually, the paired sperm masses hidden within the spermatophores are small, and there has been a co-evolution of spermatophores and those parts of the female genitalia which are used to pick up the spermatozoa and to store spermatozoa. These are structures like specialized sclerotizations, glands or, in a few species, seminal receptacles which are hidden inside the genital atrium (or uterus externus). In most species there are paired erectile bodies, homologous to genital appendages, which are attached to the dorsal side of the genital operculum which also is part of an appendage homologon. All these structures vary among genera and families. The comparison of spermatophores and genitalia of different species belonging to most genera and families suggest that the female gonopods consist primarily of paired cushion-like structures, each equipped with a small finger-like appendage vestige. These appendage vestiges are retained in many species, particular in the Charinidae and Charontidae. They are erectile by increase in blood pressure, and they are thereby probably bent in characteristic ways and thus can pull off the sperm masses from the spermatophore. In some Charinidae, and in some species of *Damon* and *Phrynichus* (Phrynida, Phrynichidae) these appendage vestiges are totally lost. In the Phrynidae, on the other hand, they have become sclerotized and hard. They form the well-known claw-like sclerites, and an invagination at the base of each sclerite has been shaped to form a true seminal receptacle. Similar genitalia have evolved convergently in the genus *Trichodamon* (Phrynida, Phrynichidae). Spermatophores and the corresponding female genitalia and their mechanisms of a number of genera from most families are described and illustrated.

Whip spiders transfer spermatozoa by means of stalked spermatophores (Alexander 1962a, b; Klingel 1963; Weygoldt 1969). After a prolonged courtship dance which the male performs in front of the female, he turns around until facing the same direction as the female and standing in front of her. In this position he deposits a spermatophore and attaches its stalk to the substratum. Thereafter he turns around to face the female and lures her toward the spermatophore. The female then steps over the spermatophore and picks up the sperm.

The spermatophores are large and complex structures. They consist of a stalk, a spermatophore head and paired sperm masses or, in other species, sperm packages. Each individual spermatozoon is rolled up and encapsulated, and the globular cells are either glued together or surrounded by secretion. The sperm masses are small when compared to the size of the total spermatophore. Spermatophore morphology varies between species,

genera and families, and the same is true for the female genitalia, in particular for those structures which are used to pick up the spermatozoa. After sperm transfer, an empty spermatophore is left behind or, in a few species, is eaten either by the male or the female.

The distal genitalia of a whip spider of either sex are composed of a large genital atrium, homologous to the uterus externus of spiders, a large genital operculum, and paired erectile bodies attached to the dorsal or inner side of the genital operculum (Weygoldt et al. 1972). These erectile bodies are considered to be homologous to genital appendages, to the endopods of the opisthosomal appendages of eurypterids or xiphosurids (Pocock 1894; Werner 1935; Weygoldt 1970); they are therefore termed gonopods here. The genital operculum with its lateral book lungs is homologous to the genital operculum of xiphosurids and eurypterids which is part of the same pair of appendages, the book lungs or, in xiphosurids the book gills, representing the exopods.

In the male, the gonopods are two-segmented. They form an unpaired complex structure provided with muscles and haemolymph spaces and a complex central cavity which acts as a mold for the formation of the spermatophore head. It also contains grooves through which the secretions from several large glands can be lead to the exterior in order to attach the spermatophore stalk to the ground. Kraus (1970) suggested that the shape of the male genitalia could provide useful characters for taxonomy. The problem is that the shape of these organs depend heavily on the state of preservation. Genitalia of two males of the same species sometimes appear much more different from each other than those from two males of two different species. The spermatophores formed in these male genitalia are complex and diverse. Their sperm masses are located at various positions within the spermatophore head. Unfortunately the spermatophores of only a limited number of species are known. They will be described subsequently.

The female genitalia are much simpler. The genital atrium contains specialized sclerotizations which vary among species, glandular structures and various structures used for sperm storage. Even true seminal receptacles have evolved convergently in some groups. The gonopods are cushion-like structures with or without vestiges of the appendage telopodids. These telopodids, here termed appendage vestiges, are used to pick up the sperm mass from the spermatophores. Their morphology varies considerably between species, genera and families. Just as with male copulatory organs, there has been a co-evolution of spermatophores and female genitalia.

All whip spiders will mate several times if they have the chance. The females become unreceptive once oogenesis has reached a certain stage. All whip spiders are long-lived and continue to molt and to grow after having reached sexual maturity. During molting, the females loose all stored spermatozoa—which remain in the shed storage organs. The females become receptive again soon after molting.

In the following discussion I will demonstrate different types of spermatophores and the corresponding female genitalia and describe how these are used to pick up the sperm masses and how they have evolved within the

taxon Amblypygi. As to the function, most of my description is inferred from the morphology of the structures. Many whip spiders are unable to walk and to mate on glass; therefore, direct observation is impossible.

As a base for the discussion of the evolution of genitalia I use the cladogram and system of Weygoldt (1996a, b) (Table 1). In this system, the African genus *Paracharon* is considered the sister group of the remaining amblypygids, the Euamblypygi. This group is divided into two taxa, the Charinidae and the Neoamblypygi. The Charinidae is mainly characterized by plesiomorphies; I have not found convincing synapomorphies. All charinid genera are in urgent need of revision. In particular, it is not clear whether *Charinus* Simon 1892 is a monophyletic group and whether *Charinides* Gravely 1911 should be considered a junior synonym of *Charinus* as Delle Cave (1986) assumes. The Neoamblypygi, however, is united by several synapomorphies. It contains the taxa Charontidae as restricted by Quintero (1986) and the Phrynida or Apulvillata, and these are divided into the Phrynidae and Phrynichidae, both characterized and united by convincing synapomorphies.

## RESULTS

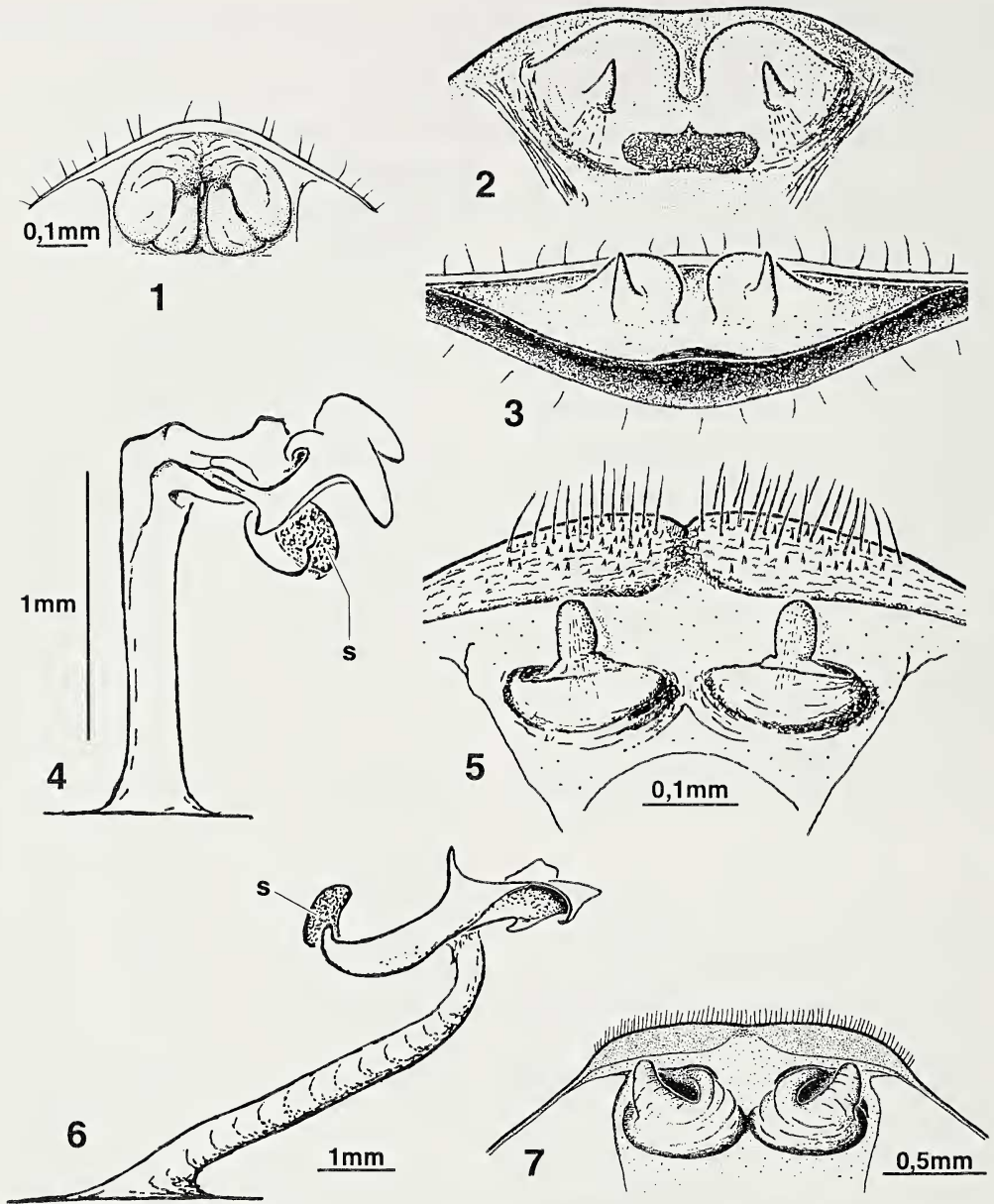
***Paracharon*.**—According to the taxonomic analysis, *Paracharon caecus* Hansen 1921 is the most plesiomorphic species and the adelphotaxon of all remaining Amblypygi, the Euamblypygi. Its female gonopods are simple soft cushions (Fig. 1). Spermatophores are not known, therefore the function of the gonopods are unclear; and it is also unclear whether the simple gonopods are plesiomorphic or the result of simplification.

**Charinidae and Charontidae.**—Gonopods with a soft, finger-like appendage vestige (Fig. 2, 3) are found in many charinid and charontid whip spiders. They are probably synapomorphic for the Euamblypygi or, if the genitalia of *Paracharon* are secondarily simplified, for all Amblypygi.

Such finger-like appendage vestiges as shown in Fig. 2, 3 for *Charinus koepkei* Weygoldt 1972c may be short and pointed as in this case and in *Charinides bengalensis* Gravely 1911 or much longer as in several other *Charinus* species, e.g., *Charinus africanus* Hansen 1921 (Weygoldt 1972a). The

Table 1.—The amblypygid genera, their relationships according to Weygoldt (1996a and 1996b), their distribution, and species numbers. The species numbers for many genera are guesses based on descriptions from the last century. Only for the Phrynidae and Phrynichidae can reliable data be given; they are based on the revisions of Mullinex (1975), Quintero (1981, 1983, a few more species have been described since then), Weygoldt (1998) and the author's unpublished data on *Damon*.

		Genera	Distribution	No. of species
		<b>Paracharon</b>	W. Africa	1
	Charinidae	<b>Sarax</b>	S.-E. Asia	4(?)
		<b>Phrynichosarax</b>	S.-E. Asia	5(?)
		<b>Charinus</b>	world wide	>20
		<b>Charinides</b>	circumtropic	5(?)
		<b>Tricharinus</b>	neotropic	3
		<b>Catageus</b>	S.-E. Asia	1
	Charonidae	<b>Charon</b>	S.-E. Asia	>4
		<b>Stygophrynus</b>	S.-E. Asia	6(?)
	Phrynidae	<b>Acanthophrynus</b>	Mesoamerica	1
		<b>Phrynus</b>	Mesoamerica	>16
		<b>Paraphrynus</b>	Mesoamerica	>12
		<b>Heterophrynus</b>	S. America	10(?)
	?	<b>Xerophrynus</b>	S.-E. Africa	1
	Phrynichidae	<b>Phrynichodamon</b>	S.-E. Africa	1
		<b>Damon</b>	Africa	10
		? <b>Musicodamon</b>	N. Africa	1
		<b>Trichodamon</b>	S. America	2
		<b>Phrynichus</b>	Africa, Asia	14
		<b>Euphrynichus</b>	Africa	2



Figures 1-7.—Female genitalia and spermatophores of some charinid and charontid Amblypygi. 1. Female genitalia of *Pracharon caecus*; dorsal aspect; 2. Female genitalia of *Charinus koepkei*, dorsal aspect; 3. Same, posterior aspect (from Weygoldt 1972c); 4. Spermatophore of *Sarax sarawakensis* in lateral view; 5. Female genitalia of *Sarax sarawakensis*, dorsal aspect; 6. Spermatophore of *Stygophrynus longispina*; 7. Female genitalia of *Stygophrynus longispina*, dorsal aspect. (s = sperm mass).

actual appearance may vary between specimens, depending on the state of preservation or on haemolymph pressure during preservation. For most species, spermatophores are not known. It is most likely that the finger-like appendage vestiges of the gonopods can be elongated or erected by an increase in hae-

molymph pressure and withdrawn by muscles, and that they are bent and strengthened in a species specific way and thus can pull off the protruding sperm masses during sperm transfer.

However, a few examples have been studied. In *Sarax sarawakensis* (Thorell 1888)

(Charinidae), the spermatophore head is complex, with paired wing-like appendages of which the functional significance is obscure. They probably provide the necessary stimuli for the gonopods to find the two protruding sperm masses (Fig. 4) (Weygoldt 1990). The inactive gonopods are rounded in this species (Fig. 5), but it is likely that they can also be elongated and pull off the sperm masses during sperm transfer. The situation is similar in *Stygophrynus longispina* Gravely 1915 (Neoamblypygi, Charontidae). Its spermatophore (Fig. 6) (Weygoldt 1990) also carries two protruding sperm masses. They are mounted on the distal ends (viewed from the male) of the spermatophore head. The spermatophore stalk is inserted at about the center of the spermatophore head. Thus, when the female presses down the proximal end of the spermatophore head with her genital operculum, the distal end will raise and move the sperm masses into the female gonopore. The folded appearance of the female genitalia and its appendage vestiges (Fig. 7) suggest that these can be inflated considerably and can tear off the sperm packages during sperm transfer.

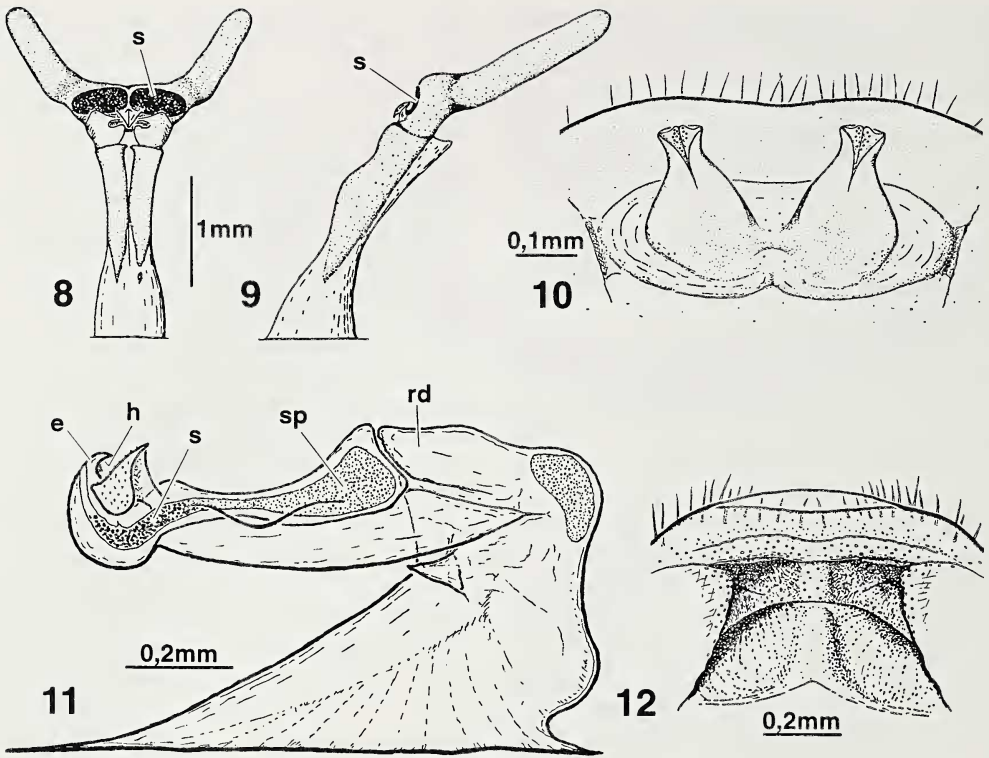
*Charinus* is a large genus distributed circumtropically over all continents and also occurring on islands, even volcanic ones like Galapagos. Some species have evolved different spermatophores, different genitalia and different means of sperm transfer. In the Brazilian species *C. brasiliensis* Weygoldt 1972 and *C. montanus* Weygoldt 1972, the appendage vestiges of the genitalia are enlarged and thickened and have the appearance of sucker-like or prehensile structures (Weygoldt 1972a, b) (Fig. 10). They can be extended by increase in haemolymph pressure and retracted by strong muscles. The spermatophores are also different. They are quite simple (Figs. 8, 9), and the spermatozoa do not form compact, protruding sperm masses but flat layers at the base of the spermatophore head (Weygoldt 1972b, 1974a). The female picks up the spermatozoa by means of her sucker-like genitalia. They are then stored in two distal cavities of the genital atrium directly behind the ends of the genitalia.

The situation is even more different in *Charinus seychellarum* Kraepelin 1898. The genitalia are reduced to flat cushions in front of which the floor of the genital atrium and its roof are strongly sclerotized. There is no

erectile appendage vestige. Further, the posterior margin of the genital operculum is transparent and forms a hard and sharp edge (Fig. 12). The spermatophore is unique among amblypygids (Fig. 11). There is a strong, triangular stalk which firmly attaches the structure to the ground, even to sand. The spermatophore head consists of a flat plate carrying two strong sperm packages, each with a spacious sperm reservoir and an opening at its tip. This tip is bent upwards and forms an embolus armed with two small hooks. The reservoirs of both sperm packages join proximally; here they contain no spermatozoa but a swelling substance which, on contact with aqueous solutions, presses out the spermatozoa stored distally. This is one mechanism. There is another, more important mechanism: The flat plate carrying the sperm packages acts as a spring. If the whole structure is bent upwards distally, it arrests at about 45°, and two rod-like structures at the upper part of the spermatophore stalk act as pistons pressing out the sperm masses. During sperm transfer, the female attaches the sharp edge of the margin of her genital operculum under the hooks of the emboli and then bends the sperm package upwards. The spermatozoa are thereby emptied into the genital atrium and stored between the roof of the atrium and a dorsal fold.

**Phrynida.**—The situation in the Phrynida or Apulvillata is much clearer. This taxon contains two families, the Phrynidae and the Phrynichidae.

**Phrynidae.**—In the Neotropical Phrynidae, the female gonopods are equipped each with a claw-like, hard and dark sclerite (Fig. 13). These sclerites have long been known and termed cocoon-holders by Börner (Werner 1935). They have, however, nothing to do with the transportation of the egg sac. The sclerites can be elevated by increase in haemolymph pressure. They are further equipped with a strong adductor muscle which, by superficial view, seems to be attached to a deep apodeme. However, at the base of each sclerite there is an invagination leading into a spacious seminal receptacle (Fig. 14). The apertures of these receptacles are covered by the sclerite bases, and the adductor muscles are attached to the walls of the receptacles (Fig. 15). Contraction of these muscles, thus, leads to the adduction of the sclerites and at the



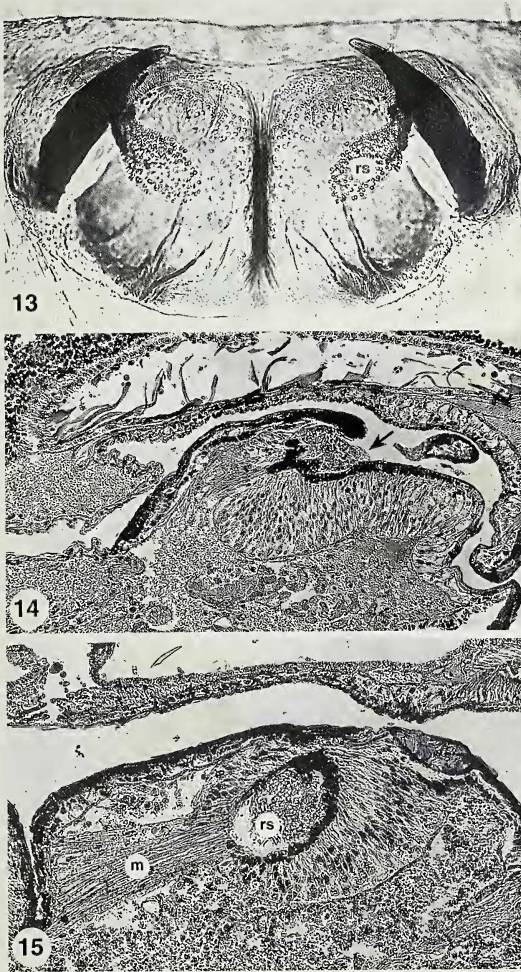
Figures 8–12.—Spermatophores and female genitalia of two species of *Charinus*. 8. Spermatophore of *C. brasilianus*, anterior view; 9. Same, lateral aspect; 10. Female genitalia of *C. brasilianus*, dorsal aspect (from Weygoldt 1972b); 11. Spermatophore of *C. seychellarum*, lateral view; 12. Female genitalia of *C. seychellarum*, dorsal aspect. Abbreviations: e = embolus, h = hooks, rd = rod-like structure which compresses the sperm package when the tip is lifted upwards. Abbreviations: s = sperm mass, sp = sperm package).

same time widens the seminal receptacles. The walls of the receptacles are punctured by many glandular pores. Nutrients or other substances are probably released through these pores and nourish or otherwise maintain the spermatozoa (Weygoldt et al. 1972).

The males of the Phrynidae produce large spermatophores with triangular, heavily sculptured spermatophore heads (Weygoldt 1969, 1972b, 1974b, 1977) (Figs. 16, 17, 19, 20). The formation of these complex spermatophores takes quite long, 10–20 minutes. After spermatophore formation, the male turns toward the female again and touches for another 10 minutes the spermatophore with his pedipalps and chelicerae. The meaning of this behavior is still obscure. The attachments of a pheromone may be one possibility, the deposition of an enzyme to soften the sperm packages another. The spermatophore contains two comparatively small sperm-packages hidden

deeply among the sculpturing (Figs. 17, 18, 19, 21), and two arm-like distal extensions act as conductors leading towards the sperm-packages. The female pulls out these sperm-packages by means of her claw-like sclerites, and the sperm is thereby sucked into the seminal receptacles. In *Phrynus marginemaculatus* C.L. Koch 1841, the sperm packages are attached to small plates, and these plates are visible pressed underneath the claw-like sclerites after sperm transfer.

The sculpturing varies among species and also the shapes of the arm-like appendages; and they may even be forked or T-shaped. The functional significance of these differences is obscure, in particular since the female genitalia are quite uniform. We may assume that the different sculpturings aid the female in recognizing the spermatophore and finding the sperm packages. Another point may be that the sculpturing creates a large, hard, elastic



Figures 13–15.—Female genitalia of *Phrynia marginemaculatus*; 13. Dorsal aspect of genitalia of an exuvia with the claw-like sclerites; 14. Longitudinal section through one of the gonopods with the entrance to the seminal receptacle (arrow); 15. Cross section through one of the gonopods with the seminal receptacle containing spermatozoa. Abbreviations: m = muscle, rs = seminal receptacle (from Weygoldt et al. 1972).

spermatophore head with a minimum of material. Even the stalk is created with a minimum of material; it is not solid as may seem from Figs. 16 and 20 but its cross section is V-shaped instead.

This unique system featuring spermatophores with complexly sculptured spermatophore heads and female gonopods equipped with claw-like sclerites and seminal receptacles is one of the autapomorphies of the Phryniidae. The features are found with little

variation in all four genera and in all species (Mullinex 1975; Quintero 1981; Weygoldt 1972b, 1974b, 1977).

**Phrynichidae.**—The Phrynichidae are much more variable as far as their spermatophores and genitalia are concerned.

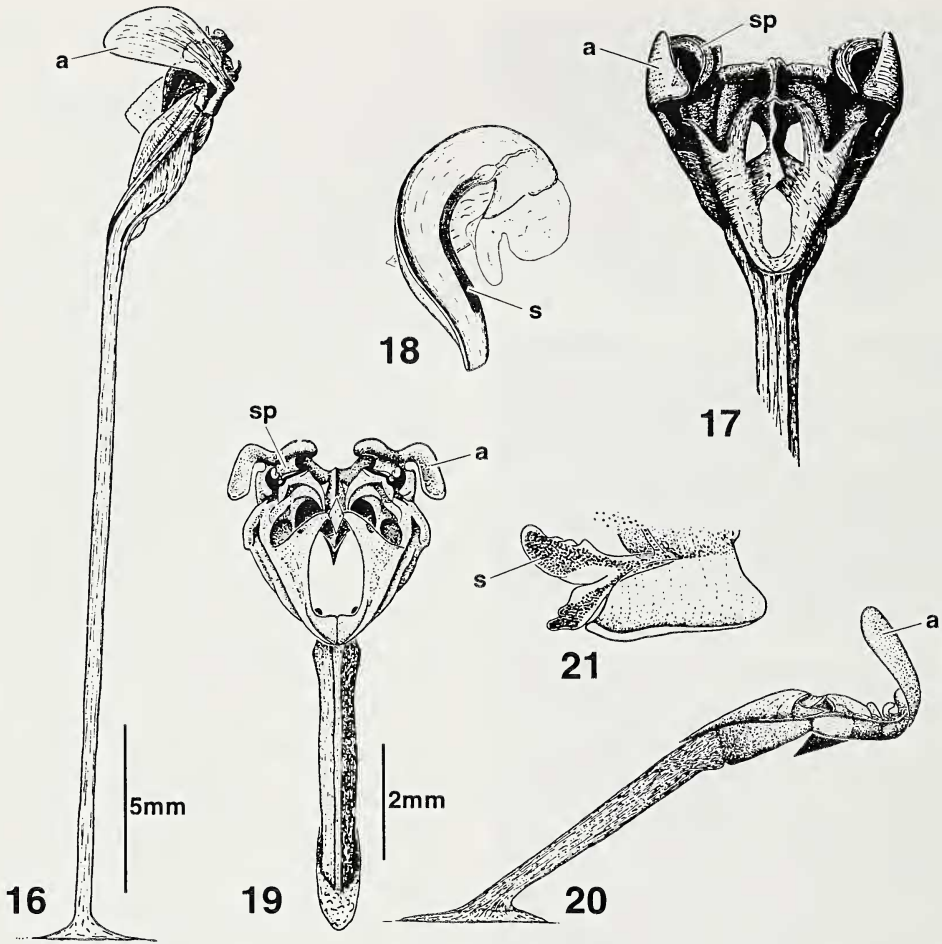
*Phrynichodamon scullyi* (Purcell 1911) is a primitive species and the sister taxon of all other Phrynichidae (Weygoldt 1996a) (with the exception of *Xerophrynus* Weygoldt 1996, which is tentatively considered a basal offshoot of the Phrynichidae, Table 1). Spermatophores and genitalia of this species resemble the situation found in charinid and charontid whip spiders. In the small and simple spermatophores, the spermatozoa form large, protruding sperm masses (Weygoldt 1998a). The female gonopods are equipped with soft, finger-like appendage vestiges which can probably be extended by haemolymph pressure and tear off the sperm masses. These are then stored underneath the appendage vestiges (Weygoldt 1996a) (Fig. 23).

It is easy to conceive that a remote ancestor of the Phryniidae had a similar system and that the appendage vestiges became sclerotized and hard and the place at the base of these vestiges invaginated to better store the spermatozoa.

The remaining phrynichids, however, evolved into another direction. In *Damon*, and convergently in most Phrynichinae, the appendage vestiges were lost.

Some of the western species of *Damon* still have appendage rudiments. In *Damon johnstonii* (Pocock 1894) (Fig. 24) and in *Damon tibialis* (Simon 1876) there is a small appendage rudiment which has, perhaps, a sensory function; nothing is known about spermatophores and sperm transfer in these species.

Another undescribed species from Cameroon has evolved very different genitalia. The gonopods are enlarged hook-like structures which are strongly sclerotized and black (Fig. 25). Again, nothing is known about spermatophores and sperm transfer, but these genitalia strongly suggest that the spermatophores are very different from those of other *Damon* species. This species may be the sister taxon of the Phryniidae, in which case the Phrynichidae form a paraphyletic group. But this is unlikely. The *Damon* species are united by clear synapomorphies, and the genitalia of this *Damon* species and of the Phryniidae are only



Figures 16–21.—Spermatophores of two species of the Phrynidae. 16. Spermatophore of *Heterophrynus longicornis*, lateral view; 17. Anterior view of spermatophore head; 18. Right sperm package enlarged (from Weygoldt 1972b); 19. Spermatophore of *Phrynus marginemaculatus*, anterior view; 20. The same, lateral view; 21. One of the sperm packages enlarged (from Weygoldt 1969). Abbreviations: a = arm-like distal extension, s = spermatozoa, sp = sperm package.

superficially similar. There is no claw-like sclerite on a soft cushion-like gonopod with seminal receptacles, but the tip of the gonopod is sclerotized. It is more likely that this similarity is the result of convergent evolution.

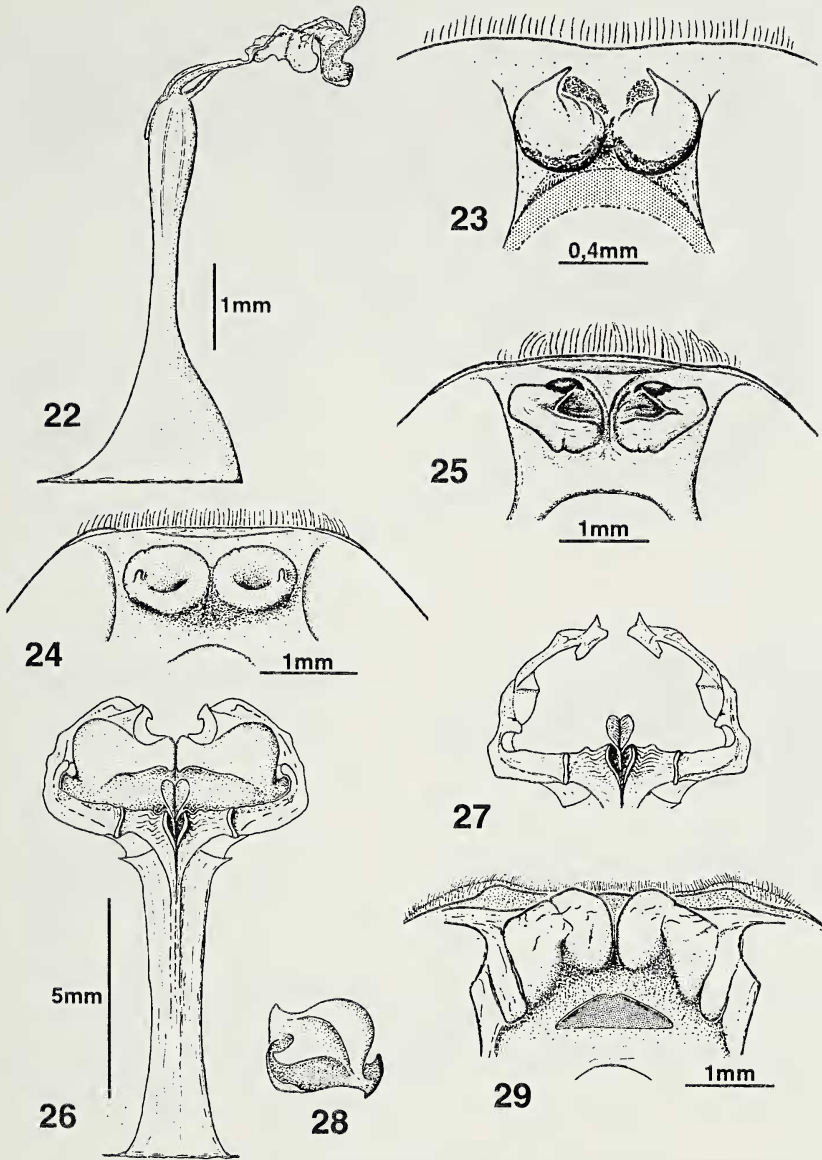
*Damon medius* (Herbst 1797), another West African species, has its lost gonopodial appendage vestiges. The gonopods are large cushions with a deep dorsal depression. They look more like a depression surrounded by large walls which join in the midline.

In all East African species of *Damon*, the female genitalia are flat cushions without any appendage vestiges. They are supported by an anterior sclerotized plate or bar (Fig. 29).

These cushions are used to detach large sperm-packages from the spermatophore (Weygoldt 1998a; Weygoldt & Hoffmann 1995) (Figs. 26–28). The sperm packages are so large that they fill out nearly the complete genital atrium. This is a specialty of this *Damon variegatus* species group or of all *Damon* species; the reproductive biology of the western species is unknown. The larger parts of these sperm packages consist of a secreted mass which serves perhaps as a matrix to hold and retain the spermatozoa within the female genital atrium; seminal receptacles are missing (Weygoldt & Hoffmann 1995).

The female genitalia of the Old World

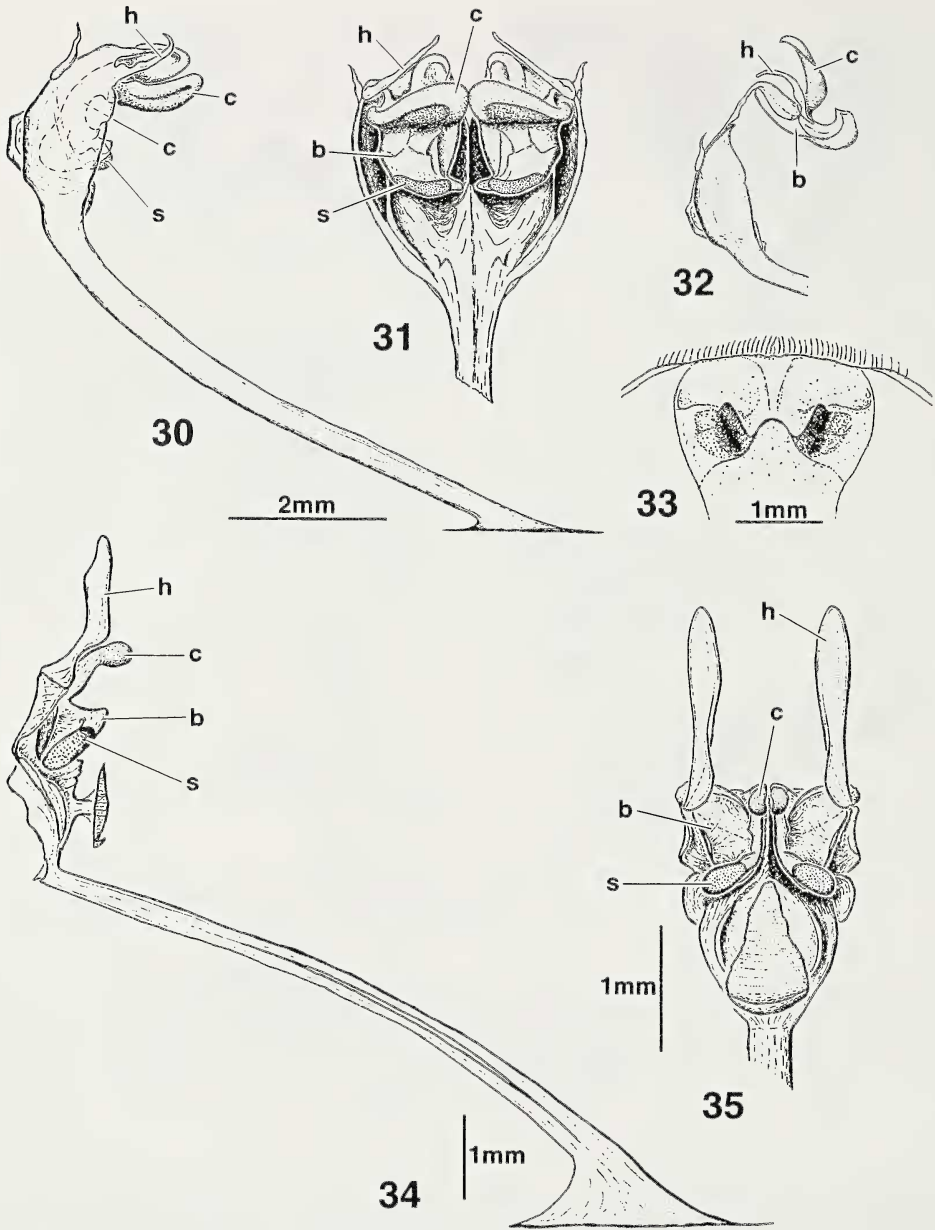




Figures 22–29.—Spermatophores of *Phrynichodamon* and *Damon*. 22. Spermatophore of *Phrynichodamon scullyi*, lateral view (from Weygoldt 1998a); 23. Female genitalia of *Phrynichodamon scullyi*, dorsal aspect (from Weygoldt 1996a); 24. Female genitalia of *Damon johnstonii*, dorsal aspect; 25. Female genitalia of undescribed *Damon* species, dorsal aspect; 26. Spermatophore of *Damon diadema*, anterior view; 27. Anterior view of spermatophore head of emptied spermatophore; 28. One of the sperm packages; 29. Female genitalia of *Damon diadema*, dorsal aspect (from Weygoldt & Hoffmann 1995).

Phrynichinae, the genera *Phrynichus* and *Euphrynichus*, are simple cushion-like elevations which, in some species, have partly sclerotized walls or tooth-like sclerotized tips (Fig. 33). There are no seminal receptacles; the spermatozoa are stored inside the genital atrium. The spermatophores of all Phrynichinae are complex and unique. Their spermatophore

heads consist of an outer frame and two inner bars, each carrying a compact sperm mass at its proximal end (Figs. 30, 31, 34, 35). At the distal end of the spermatophore head there are arms or levers and, at the basis of these, cushions. If these levers or the cushions are pressed down, the bars carrying the sperm masses are elevated (Weygoldt 1998a; Wey-

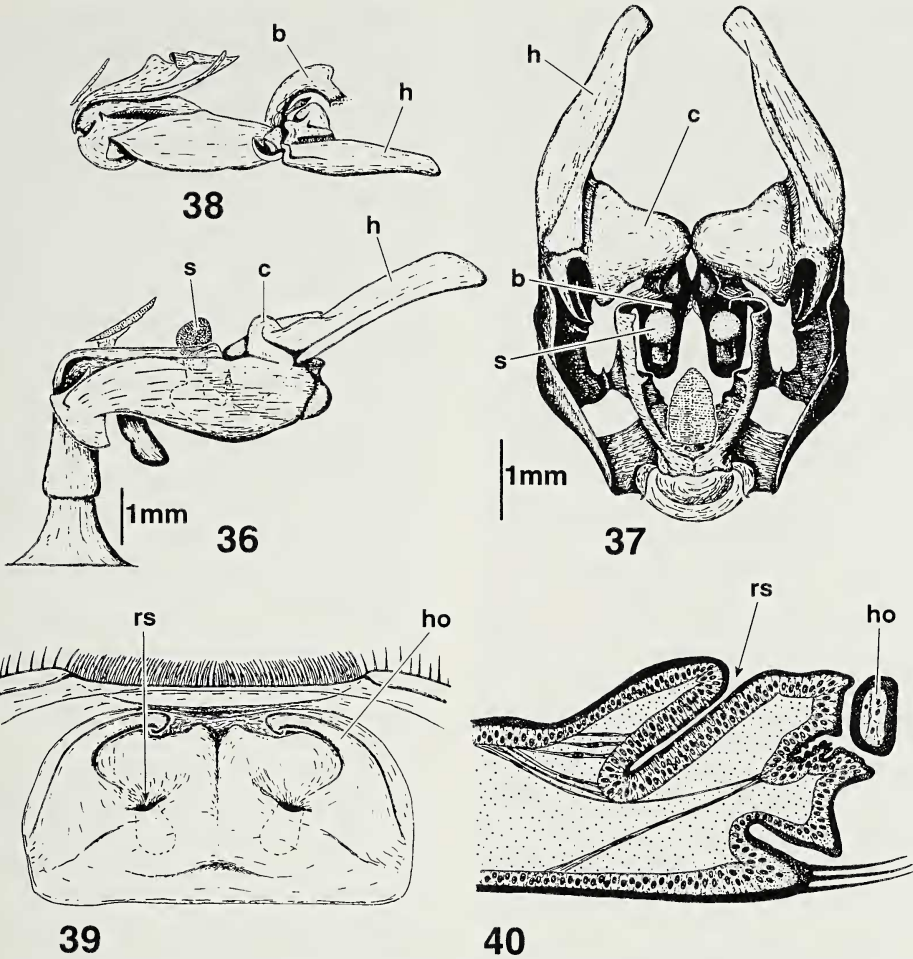


Figures 30–35.—Spermatophores of *Phrynichus* and *Euphrynichus*. 30. Lateral view of total spermatophore of *Phrynichus ceylonicus*, 31. Dorsal aspect of spermatophore head of same; 32. Spermatophore head of emptied spermatophore (from Weygoldt & Hoffmann 1995); 33. Female genitalia of *Phrynichus ceylonicus*, dorsal aspect (from Weygoldt 1998b); 34. Lateral view of total spermatophore of *Euphrynichus bacillifer*; 35. Dorsal aspect of spermatophore head (from Weygoldt 1998a). Abbreviations: b = bar carrying sperm mass, c = cushion, h = lateral horn, s = sperm mass.

goldt & Hoffmann 1995) (Fig. 32) and the sperm masses can be grasped by the female gonopore.

*Trichodamon froesi* Mello Leitão 1940, a member of the only New World phrynichid

genus, has female genitalia which bear some similarity to those of the Phrynidae (Weygoldt 1977). The gonopods are soft cushions with a hook-like appendage vestige, and close to each hook there is a small seminal receptacle



Figures 36–40.—Spermatophore and female genitalia of *Trichodamon froesi* (from Weygoldt 1977). 36. Lateral view of total spermatophore; 37. Dorsal aspect of spermatophore head; 38. Lateral view of emptied spermatophore head; 39. Female genitalia, dorsal aspect; 40. Longitudinal section through one of the gonopods. Abbreviations: b = bar carrying sperm mass, c = cushion, h = lateral horn, ho = hook-like structure, rs = seminal receptacle, s = sperm mass.

(Figs. 39, 40). The spermatophore of this species is composed of the same parts as those of the Old World Phrynichinae and have the same mechanism, but they are stronger, with a short and stout stalk and a strong outer frame (Figs. 36–38). If the large cushions are pressed down, the bars carrying the sperm masses are lifted and finally arrested (Fig. 38). The hook-like appendage vestiges are probably used to grasp around the bases of the sperm masses and lead them into the seminal receptacles.

#### DISCUSSION

Courtship behavior is similar in all whip spiders observed; and, although there are

spectacular variations, it will not be discussed here in detail. One of the characteristic features of the Amblypygi is the fact that the male turns away from the female during spermatophore formation. The Amblypygi share this behavior with the Uropygi; in other arachnids which deposit spermatophores, the male faces the female during spermatophore production. This characteristic behavior can be assumed to be synapomorphic either for the Pedipalpi (Uropygi and Amblypygi) or for the Megopericulata (Uropygi, Amblypygi and Araneae). I believe, and Alexander & Ewer (1957) do also, that this latter possibility is the correct one. As a consequence, we have to assume that spiders lost this behavior—per-

haps better, changed this behavior—in the course of the evolution of their characteristic indirect-direct method of sperm transfer. Alexander (1962a, b) was the first to observe mating in amblypygids. She described spermatophore formation as a two step process: The male first deposits an empty spermatophore, then turns to the female again and fills the spermatophore with spermatozoa. Alexander & Ewer (1957) used this two step process to understand the evolution of mating behavior in spiders. In some spiders, the male courts the female for a while, then interrupts courtship in order to fill his palpal copulatory organs. Thereafter he turns toward the female again and resumes courtship. In other species, the filling of the copulatory organs and courtship are two completely separated behavior acts. The behavior of the male whip spider, in which he turns away from the female to produce an empty spermatophore, was hypothesized by Alexander & Ewer (1957) to have been the initial step leading to the reproductive behavior of spiders. However, the observation of Alexander is incorrect. I have now observed and videotaped the behavior of several species of *Damon*, including *D. variegatus*, the same species Alexander observed. In all amblypygid species observed, the spermatozoa are firmly built into the spermatophore as soon as the male lifts his body and starts to turn towards the female again. We can, of course, still assume that a behavior by which the male turns away from the female before spermatophore formation was the initial step from which spider mating behavior evolved.

Male and female genitalia, or spermatophores and female genitalia, have evolved as means to successfully transfer sperm and thus ensure insemination. I assume that they have been shaped by sexual selection in the sense of Eberhard (1985). It is evident from these few examples of Amblypygi that the co-evolution of spermatophores and female genitalia has led to different structures and mechanisms. It is also evident that the structures vary among genera and families and that they can be used as characters in systematic research.

The comparative approach demonstrated here helps to understand the origin and evolution of complex genitalia such as those of *Trichodamon* or of the Phrynidae with their claw-like sclerites and seminal receptacles.

The genitalia also provide useful characters for taxonomy. For example, all Phrynidae are characterized by gonopods with claw-like sclerites and seminal receptacles. Species without this morphological arrangement cannot belong to the family Phrynidae unless it can be shown that the species in question shares other synapomorphies with the Phrynidae and has not yet evolved the typical genitalia, or that it has reduced these structures. Thus, the Namibian *Xerophrynus machadoi* (Purcell 1901) which had been described as *Paraphrynus machadoi*, has female genitalia different from those of all phrynids and, in fact, different from those of all other species. Because of other characters, this species is probably a remote plesiomorphic member of the Phrynichidae (Weygoldt 1996a). Unfortunately, the reproductive biology of this desert-adapted species is not known. In captivity it refuses to produce a spermatophore; perhaps reproductive behavior is triggered by a complex set of environmental changes. Therefore the mechanism of sperm transfer in this species has yet to be discovered.

Genitalia with claw-like sclerites and seminal receptacles are an autapomorphy of the Phrynidae. Quintero (1980) assumed that such claw-like sclerites are an autapomorphy of the Phrynida (Phrynichidae and Phrynidae) and that the Phrynichidae, with the exception of the undescribed *Damon* species, have reduced these sclerites. But this is unlikely. The *Damon* species and the Phrynichinae are united by clear synapomorphies, and the genitalia of this *Damon* species and of the Phrynidae are only superficially similar. It is more likely that this similarity is the result of convergent evolution.

There are many more open questions—in fact, there are more questions than answers. For example, the reproductive biology and the exact systematic position of *Muscodamon atlanteus* Fage 1939 within the Phrynichidae is unknown. This species is known from only four badly-preserved museum specimens.

The situation is even worse in the Charinidae. Although many species have the typical gonopods with a finger-like appendage vestige, some lack them. The Brazilian species of *Charinus* possess sucker-like gonopods, and those of *Charinus seychellarum* are even more different. The spermatophore and female genitalia of this species are unique among ambly-

pygids. The spermatophore resembles those of some pseudoscorpions or whip scorpions (Uropygi). It came as a surprise to find such different spermatophores within one genus, and it is hard to believe that species with such different genitalia should be found in the same genus. The gonopods of *Tricharinus* Quintero 1986 are also different. Quintero (1986) published SEM pictures which reveal similar details to my own unpublished light microscopy studies. The mechanism of these gonopods remain unknown, as the spermatophores are not known; and there are no histological data. The various spermatophores and genitalia in different *Charinus* species and their relatives may suggest that this genus is a paraphyletic or even polyphyletic assemblage, and the fact that the Charinidae as a whole are not characterized by synapomorphies shows that studies of the reproductive biology and the associated structures of these genera are urgently needed and that there is ample work to do for the next generation.

Another unsolved question is the functional significance of various part of the complex spermatophore heads. Perhaps studies with larger numbers of specimens, some of which may produce spermatophores with slight morphological differences, may lead to an understanding of female choice and sexual selection. Sexual selection and sperm competition have never been studied in any whip spider, and the meaning or information content of the different behavior elements during courtship or fighting are completely obscure.

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